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Dehydration accelerates respiration in postharvest sugarbeet roots

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ABSTRACT

Sugarbeet (*Beta vulgaris* L.) roots lose water during storage and often become severely dehydrated after prolonged storage and at the outer regions of storage piles which have greater wind and sun exposure. Sucrose loss is known to be elevated in dehydrated roots, although the metabolic processes responsible for this loss are unknown. To identify processes that contribute to sucrose loss in dehydrated roots, respiration rate, cellular electrolyte leakage, and sucrolytic enzyme activities were determined in roots of two varieties (VDH 66156 and Beta 4797R) during 4 weeks of 10 °C storage at high (85%) and low (40%) relative humidities. Roots stored at 40% relative humidity dehydrated significantly and lost almost 50% of their weight after 4 weeks of storage. Electrolyte leakage increased in these roots, indicating that dehydration damaged cellular membranes. Respiration rate generally increased in roots stored at 40% relative humidity compared to roots stored at 85% relative humidity. The increase in respiration rate was positively correlated with root weight loss and electrolyte leakage. Respiration rate was most closely associated with electrolyte leakage, however, suggesting that elevations in respiration rate were not due to dehydration, but to the membrane damage that occurred in response to dehydration. Activities of the sucrose-degrading enzymes, sucrose synthase, alkaline invertase and soluble acid invertase, were unaltered by dehydration. Alterations in sucrolytic enzyme activities, therefore, were not needed to provide for the increased demand for respiratory substrates in dehydrated roots. These results suggest that storage at low relative humidity alters the postharvest physiology of sugarbeet roots by increasing the rate of weight loss, reducing membrane integrity, and accelerating root respiration rate.

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1. Introduction

Sugarbeet (*Beta vulgaris* L.) roots produced in northern growing regions of North America, Europe and Asia are typically stored in large outdoor piles for up to 200 d prior to processing (Campbell and Klotz, 2006). Roots stored in these piles are cooled by ambient winter air, either passively or actively by circulating air through ventilation pipes placed beneath the piles. The flow of cold winter air through storage piles inevitably causes root dehydration. Root dehydration begins immediately after harvest and generally increases with storage duration (Dexter et al., 1969). Dehydration is particularly severe in "rim beets", i.e., the roots that populate the outermost 60 cm of piles, since these roots are exposed to sun, wind, and freeze/thaw cycles that damage cellular membranes (Tungland et al., 1998). Weight losses of up to 40% have been observed in rim beets during 78 d in storage (Dexter et al., 1969).

Dehydration of sugarbeet roots during storage is associated with a loss of sucrose and overall root quality. Several studies have shown root sucrose content and sugar yield after processing to be negatively impacted by dehydration. In one study, sucrose loss during 103 d in storage was found to be elevated 1.5- and 2.4-fold in roots that lost 7.4 and 43%, respectively, of their fresh weight to dehydration, relative to non-dehydrated roots (Pack, 1926). Rim beets, which typically comprise 17–20% of the volume of large storage piles, can be responsible for as much as 40% of the sucrose loss during storage (Tungland et al., 1998), and up to three-fold greater loss in recoverable sucrose yield has been documented in dehydrated rim beets compared to roots in the interior of piles (Dexter et al., 1969). Elevated concentrations of the invert sugars, glucose and fructose, which impede sucrose crystallization and increase sucrose losses during processing, and reductions in root turgidity and tissue elasticity, which reduce the efficiency of root slicing and sucrose extraction operations, have also been documented in dehydrated sugarbeet roots (Wyse, 1973; Vukov and Hangyál, 1985; Tungland et al., 1998; Dutton and Huijbregts, 2006).

Although the effect of dehydration on sucrose content and quality in stored sugarbeet roots is well documented, the biochemical and physiological mechanisms responsible for these changes are unknown. In other plant systems, however, dehydration is known to cause widespread changes in gene expression, protein expression and metabolism as cells and tissues respond to reductions in turgor pressure and cell volume, increases in the concentrations of dissolved compounds, and exposure to reactive oxygen species (ROS) that are generated as part of a generalized stress response (Ingram

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and Bartels, 1996; Zhu, 2002; Rizhsky et al., 2004; Costantini et al., 2006). The changes in gene expression in response to water deficit are widespread. In *Arabidopsis* and rice (*Oryza sativa* L.), for example, water deficit alters the expression of more than 1500 and 650 genes, respectively (Rizhsky et al., 2004; Degenkolbe et al., 2009). Among the genes induced by dehydration are those involved in the synthesis of water channels, ion channels, and compounds that act as cellular osmoticums such as soluble sugars, proline, and glycine betaine (Ingram and Bartels, 1996). Defense proteins, including the antioxidant enzymes, superoxide dismutase, ascorbate peroxidase, catalase, and glutathione reductase (Jiang and Zhang, 2002; Sala and Lafuente, 2004), and cytochrome P450 genes that have been implicated in extracellular lipid synthesis and may assist in repairing membrane damage caused by ROS (Ehlting, 2006; Degenkolbe et al., 2009) are also induced.

The large-scale changes in gene expression, protein expression and metabolism that occur in water-stressed plant tissues impact the overall energy status of cells (Baena-González and Sheen, 2008). It seems likely, therefore, that dehydration responses would require an increase in respiration to generate the metabolic energy needed for these changes. The effect of dehydration on the respiration rate of stored products, however, is largely unexamined (Guevara et al., 2006), despite the known deleterous effects of respiration on postharvest plant products (Kays and Paull, 2004). In research described here, we examine the effect of dehydration on sugarbeet root respiration using roots stored at 85 and 40% relative humidities for 28 d, and examine respiratory changes in relation to root weight loss, water content, and electrolyte leakage, a measure of cellular damage (Murray et al., 1989). Since respiration in sugarbeet root is fueled principally by degradation of sucrose (Barbour and Wang, 1961) and may be responsible for the increased sucrose loss observed in dehydrated sugarbeet roots (Pack, 1926; Dexter et al., 1969; Bugbee and Cole, 1979), the activities of enzymes responsible for sucrose catabolism were also determined.

2. Materials and methods

2.1. Plant material

Two sugarbeet (*B. vulgaris* L.) varieties, VDH 66156 (Van der Have, Rilland, Netherlands) and Beta 4797R (Betaseed, Shakopee, MN, USA), were grown in a greenhouse in 15 L pots for 16 weeks with 16 h day and 8 h nights. Roots were harvested, washed, and all leaves and vegetative buds were removed. Roots were incubated for 5 d in a controlled environment chamber (Conviron model PGR 15, Winnipeg, MB, Canada) at 10 °C and 85% relative humidity to allow any harvest-incurred injuries to heal. Experiments were initiated by transferring half of the roots from each variety to a second controlled environment chamber at 10 °C and 40% relative humidity. Roots were then stored for up to 28 d at 85 or 40% relative humidity and 10 °C. Higher relative humidities were not used since they promote storage diseases (Vukov and Hangyál, 1985). Roots were relocated within chambers every 3–4 d to minimize any local temperature or relative humidity differences in chambers. The experiment was conducted with four replications per treatment per time point with two roots per replicate. Longitudinal root sections comprising approximately one quarter of the root and containing crown and root tissue that was representative of the whole root were collected after 0, 14, and 28 d in storage. Tissue samples were flash frozen in liquid nitrogen, lyophilized, ground to a fine powder, and stored at −80 °C until analysis. Root water content for each sample was calculated as the difference in weight between fresh and lyophilized samples, expressed as a percentage of the sample's fresh weight.

2.2. Root respiration rate and relative electrolyte leakage

Root respiration rate was determined at 10 °C by infrared CO_2 analysis using a LICOR 6400 gas analyzer (Lincoln, NE, USA) modified for use with a 7 L sample chamber (Haagenson et al., 2006). Respiration rates were determined after 0, 3, 7, 10, 14, 17, 21, 24, and 28 d in storage, using the same roots from each humidity treatment at each time point, with 4 replicates per treatment and 2 roots per replicate. Relative electrolyte leakage was determined after 14 and 28 d in storage. Relative electrolyte leakage was equal to the conductivity of a 15 mL 0.55 mol L^{-1} sucrose solution in which 4 root discs (1 cm × 1 cm, diameter × height) were incubated overnight at 22 °C, expressed as a percentage of the conductivity of the same solution after autoclaving for 10 min. Tissue discs were obtained from a core excised perpendicular to the root axis at the widest portion of the root and contained tissue below the epidermis and external to the central vascular cylinder of the root. Conductivity was measured with an Orion 3 Star conductivity meter (Thermo Electron Corp., Beverly, MA, USA).

2.3. Protein extraction and enzyme activity assays

Protein extracts were prepared from root tissue collected after 0, 14, and 28 d in storage, with all extraction steps conducted at 4 °C. Lyophilized root tissue was homogenized in 10 volumes (w/v) of extraction buffer containing 100 mM Hepes-NaOH (pH 7.2), 10 mM Na_2SO_3, 5 mM DTT, and 1 mM $MgCl_2$ (Klotz and Finger, 2004). The homogenate was passed through Miracloth (Calbiochem, La Jolla, CA, USA) and centrifuged at 20,000 × *g* for 20 min. The supernatant was passed through a Sephadex G-25 column equilibrated with 10 mM Hepes-NaOH (pH 7.2). Desalted extracts were used for assaying sucrose synthase, alkaline invertase, and acid invertase activities, and total protein concentration. Sucrose synthase was assayed in the direction of sucrose degradation using 100 mM Mes (pH 6.5), 250 mM sucrose, 2 mM UDP, and 25 μL enzyme extract in a total volume of 75 μL. Assay reactions were incubated at 37 °C for 30 min and were terminated by adding 300 μL Nelson–Somogyi copper reagent (Nelson, 1944). Liberated fructose was determined by the method of Nelson (1944). Control reactions assayed for activity in the absence of UDP. Assays for alkaline invertase activity contained 100 mM Hepes-NaOH (pH 8.0), 100 mM sucrose, and 100 μL enzyme extract in a total volume of 200 μL. Assays for acid invertase activity contained 100 mM sodium acetate (pH 4.7), 100 mM sucrose, and 100 μL enzyme extract in a total volume of 200 μL. Invertase assay reactions were incubated at 37 °C for 30 min and terminated by adding 300 μL Nelson–Somogyi copper reagent. Released reducing sugars were determined by the method of Nelson (1944). Enzyme extracts treated with Nelson–Somogyi copper reagent before the addition of the reaction mixture were used as controls for invertase reactions. Total protein concentration was determined using the Bio-Rad protein assay kit (Hercules, CA, USA) with bovine serum albumin as a standard.

2.4. Statistical analysis

Experiment was conducted in a completely randomized design. Analysis of variance was determined using the PROC ANOVA program of SAS (ver. 9.1, Cary, NC, USA). Mean comparisons were performed using the LSD at the 0.05 level of probability.

3. Results and discussion

3.1. Relative humidity and storage duration effects on root weight loss and water content

Roots of sugarbeet varieties, VDH 66156 and Beta 4797R, lost weight during 28 d of storage at 40 and 85% relative humidity

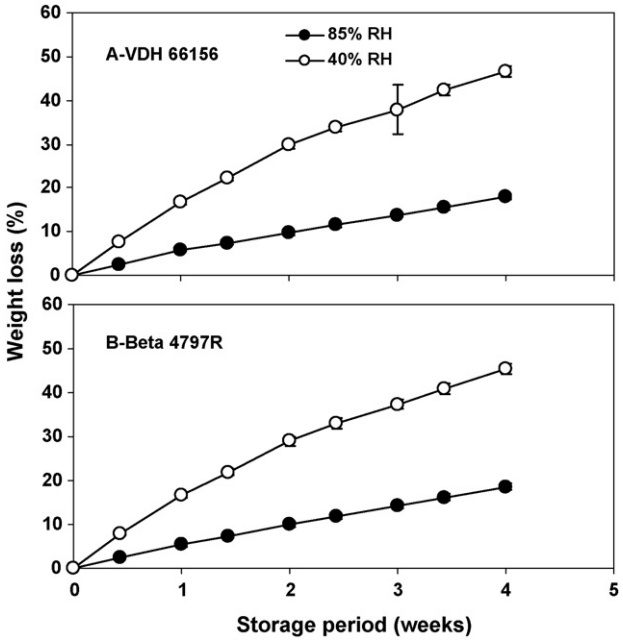

Fig. 1. Weight loss of sugarbeet roots of two varieties (VDH 66156, panel A; Beta 4797R, panel B) during storage at 85 and 40% relative humidity and 10 °C for 4 weeks. Weight loss is presented as a percentage of the weight of the root at the beginning of the experiment and was determined after 3, 7, 10, 14, 17, 21, 24 and 28 d in storage. Data are the mean ± SE of the mean ($n = 4$). $LSD_{.05}$ for panels A and B are 4.2 and 2.2, respectively.

(Fig. 1). Weight loss, expressed as a percentage of the root's weight at the beginning of the experiment, was nearly linear with time. After 28 d in storage at 85% relative humidity, roots of VDH 66156 and Beta 4797R lost 18 and 19% of their initial weight, respectively. When stored at 40% relative humidity for 28 d, these varieties lost 47 and 45% of their initial weight and were severely wilted. Weight loss was mainly due to a decrease in root water content (Fig. 2). The decrease in root water content after 28 d storage at 85% relative humidity was approximately 9 and 6% in VDH 66156 and Beta 4797R, respectively. At 40% relative humidity, the decrease in water content was approximately 31 and 25% in VDH 66156 and Beta 4797R, respectively. Although not quantified, root turgidity was greatly reduced in roots stored for 4 weeks at 40% relative humidity.

3.2. Relative humidity and storage duration effects on electrolyte leakage

The leakage of electrolytes from tissues has been commonly used as a measure of cellular membrane damage (Murray et al., 1989; Pelah et al., 1997). Electrolyte leakage was low in roots stored at 85% relative humidity for up to 28 d. Electrolyte leakage ranged from 5 to 8% in roots stored at 85% relative humidity and was not significantly different between roots stored for 14 or 28 d (Fig. 3). Elevated levels of electrolyte leakage, however, were observed in roots stored for 14 or 28 d at 40% relative humidity (Fig. 3). In roots stored at 40% relative humidity, electrolyte leakage increased 4 and 3.5-fold in VDH 66156 and Beta 4797R, respectively, after 14 d in storage and increased 7 and 5-fold after 28 d in storage.

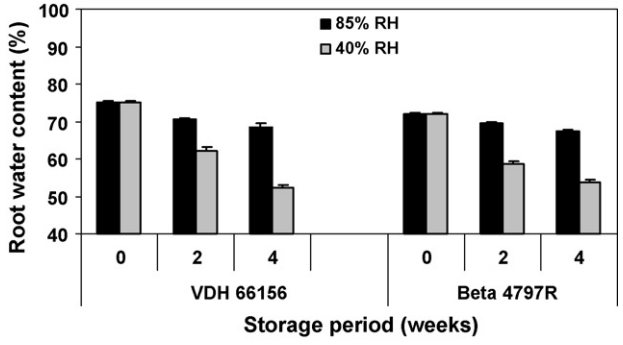

Fig. 2. Water content of sugarbeet roots of two varieties, VDH 66156 and Beta 4797R, during storage at 85 and 40% relative humidity and 10 °C for 4 weeks. Water content is expressed as a percentage of root weight. Data are the mean ± SE of the mean ($n = 4$). $LSD_{.05}$ for VDH 66156 and Beta 4797R are 2.1 and 1.7, respectively.

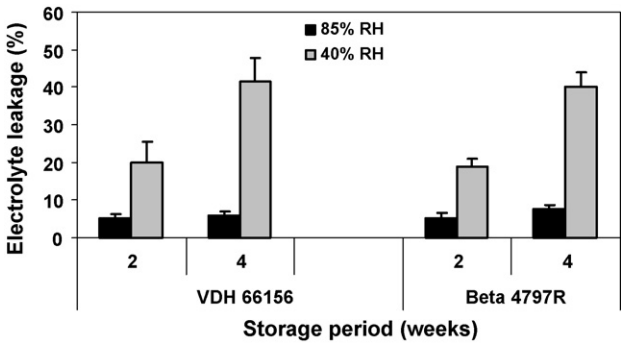

Fig. 3. Relative electrolyte leakage from root tissue of two sugarbeet varieties, VDH 66156 and Beta 4797R, during storage at 85 and 40% relative humidity and 10 °C for 4 weeks. Data are the mean ± SE of the mean ($n = 4$). $LSD_{.05}$ for VDH 66156 and Beta 4797R are 12.5 and 7.1, respectively.

The results suggest that membrane damage was minimal in roots stored at a relative humidity of 85%, even though water content declined as much as 9% (Fig. 2) and roots lost up to 19% of their initial root mass during storage (Fig. 1). Membranes were damaged, however, when water content decreased by 18% or more (Fig. 2) or roots lost 29% or more of their initial root mass (Fig. 1). Membrane damage as a consequence of dehydration has been previously reported in germinating seeds (Leprince et al., 2000) and harvested fruit (Huang et al., 2005). It is likely that dehydration-induced membrane damage is caused by reactive oxygen species (ROS), since ROS including hydrogen peroxide (H_2O_2), superoxide anion (O_2^-), singlet oxygen ($^1O_2$), and hydroxyl radical ($OH^\bullet$) are produced in response to the metabolic disruptions caused by dehydration (Sgherri et al., 1994; Jiang and Zhang, 2002), and ROS react with and damage cellular membranes (Senaratna et al., 1987; Marangoni et al., 1996).

3.3. Relative humidity and storage duration effects on root respiration

Storage at 40% relative humidity caused marked changes in the rate of sugarbeet root respiration (Fig. 4). Respiration rate in roots of VDH 66156 and Beta 4797R stored at 40% relative humidity increased significantly after 7 and 17 d in storage, respectively. Both VDH 66156 and Beta 4797R exhibited their highest respiration rates after 24 d of storage at 40% relative humidity, when respiration rate increased 108 and 82% from initial respiration rates, respectively. Respiration rate then declined with additional storage at 40% relative humidity, although respiration rate of roots stored for 28 d at 40% relative humidity was still significantly greater than that of roots stored at 85% relative humidity. In contrast, respiration rate of roots stored at 85% relative humidity, which were subjected to a slower and less severe dehydration treatment, declined slightly during 4 weeks storage. The response of respiration rate to dehydration observed in sugarbeet root is similar to that reported for postharvest grapes (*Vitis vinifera* L.; Costantini et al., 2006). In grapes, respiration rate declined in response to low levels of water loss, similar to the decline in respiration rate observed for the

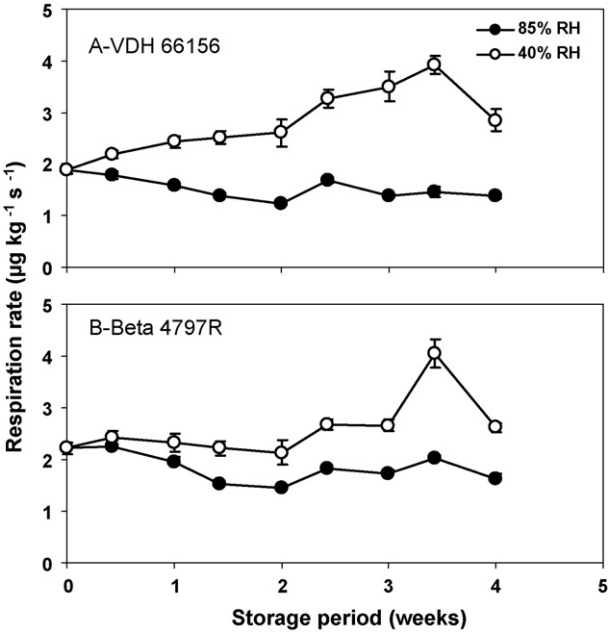

Fig. 4. Respiration rate of sugarbeet roots of two varieties (VDH 66156, panel A; Beta 4797R, panel B) during storage at 85 and 40% relative humidity and 10 °C for 4 weeks. Respiration rate was determined after 3, 7, 10, 14, 17, 21, 24 and 28 d in storage and CO_2 production is expressed in $\mu g\,kg^{-1}\,s^{-1}$. Data are the mean ± SE of the mean ($n = 4$). $LSD_{.05}$ for panels A and B are 0.39 and 0.36, respectively.

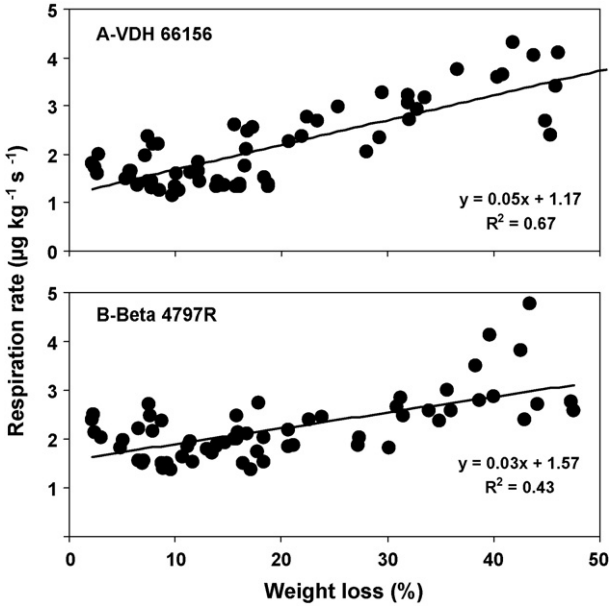

Fig. 5. Relationships between respiration rate and weight loss in roots of two sugarbeet varieties (VDH 66156, panel A; Beta 4797R, panel B) during storage at 85 and 40% relative humidity and 10 °C for up to 4 weeks. Respiration rate was measured as CO_2 production and expressed in $\mu g\,kg^{-1}\,s^{-1}$; weight loss is expressed as a percentage of the initial weight of the root prior to storage.

mildly dehydrated sugarbeet roots stored at 85% relative humidity. In general, however, grape respiration rate increased with increasing water loss, until severe water stress caused respiration rate to decline.

The results suggest that root respiration was affected by the extent of dehydration, the rate of dehydration, and genotypic responses to dehydration. For roots stored at the dehydrating conditions of 10 °C and 40% relative humidity, respiration rate changed with increasing dehydration when weight losses exceeded 17 and 33% for the sugarbeet varieties, VDH 66156 and Beta 4797R, respectively (Figs. 1 and 4). Moreover, dehydration leading to a 18–19% weight loss, which occurred in roots stored for 7 d at 40% relative humidity, was associated with an increase in respiration in roots of VDH 66156 and unaltered respiration in roots of Beta 4797R, while a similar weight loss occurring after 28 d storage at 85% relative humidity was associated with reduced respiration in roots of both varieties. This suggests that the slower dehydration that occurred at 85% relative humidity was less damaging than the more rapid dehydration that occurred at 40% relative humidity, and that both the magnitude and rate of dehydration influence root respiration rate (Figs. 1 and 4). Although both varieties dehydrated at similar rates as evidenced by their similar rates of weight loss (Fig. 1), dehydration had a greater effect on the storage respiration rate of roots of VDH 66156 than on roots of Beta 4797R (Fig. 4).

The increase in respiration rate due to dehydration is likely to have significant consequences for the storage and quality of postharvest sugarbeet roots. Respiration is the primary cause of postharvest sucrose loss in sugarbeet roots (Wyse and Dexter, 1971), and in this study, roots of VDH 66156 and Beta 4797R, respectively, lost 3.8 and 5.5% more sucrose during 4 weeks of storage at 40% relative humidity compared to storage at 85% relative humidity (data not shown). In addition, respiration is inefficient; approximately 33% of the energy released by the oxidative catabolism of sucrose is captured in the chemical bonds of ATP (Siedow and Day, 2000). The remaining energy is dissipated as heat which significantly contributes to warming of storage piles (Campbell and Klotz, 2006). As piles warm, the respiration rate of all roots and the prevalence of storage rots, including those due to *Phoma betae* Frank, *Aspergillis fumigatus* Fresen., and *Rhizopus* spp., increase (Campbell and Klotz, 2006).

3.4. Relationships of root weight loss and electrolyte leakage with respiration rate

Respiration rate was positively associated with root weight loss (Fig. 5). Despite the declines in sugarbeet root respiration rate in response to mild (Fig. 4, roots stored at 85% relative humidity) and severe (Fig. 4, roots stored at 40% relative humidity for 28 d) dehydration, respiration rate was significantly correlated with percent weight loss (Fig. 5). Percent weight loss accounted for 67 and 43% of the observed variation in respiration rate for roots of VDH 66156 and Beta 4797R, respectively. Similarly, a positive linear relationship was found for storage respiration rate and relative humidity in prickly pear cactus cladodes (*Opuntia* spp.; Guevara et al., 2006).

Root respiration rate was also positively associated with electrolyte leakage (Fig. 6). Linear relationships between electrolyte leakage and respiration rate accounted for 76 and 73% of the variation in the data for roots of VDH 66156 and Beta 4797R, respectively. Respiration rate was more closely correlated with electrolyte leakage (Fig. 6) than with root weight loss (Fig. 5), suggesting that elevations in respiration rate in roots stored at low relative humidity were not due to dehydration, per se, but to the membrane damage that occurred in response to dehydration. An increase in respiration rate in association with membrane damage has been demonstrated in other harvested plant products (Yang and Rao, 2006; Chae et al., 2007). It has been reported, however, that respiration increases prior to membrane damage, at least in dehydrated root radicles of germinating seedlings (Leprince et al., 2000). Presently, it is unknown whether the respiratory increase observed in dehydrated sugarbeet roots is coincident with or simply correlated with membrane damage.

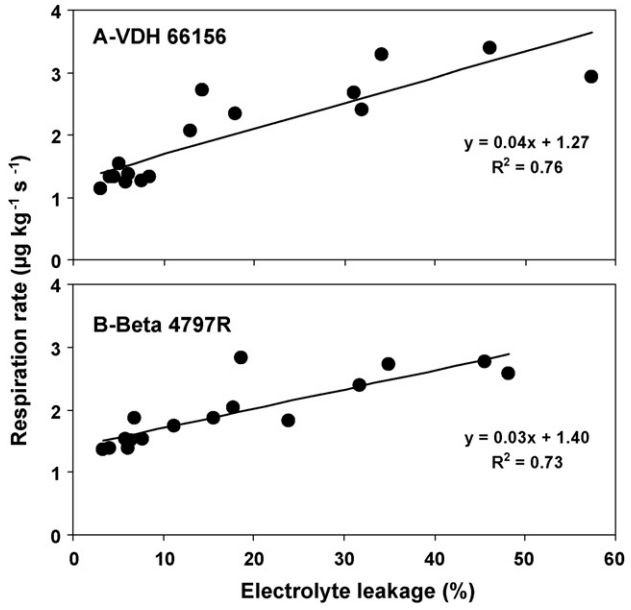

Fig. 6. Relationships between respiration rate and electrolyte leakage in roots of two sugarbeet varieties (VDH 66156, panel A; Beta 4797R, panel B) during storage at 10 °C for up to 4 weeks. Respiration rate was measured as CO_2 production and expressed in $\mu g\,kg^{-1}\,s^{-1}$.

3.5. Effect of relative humidity on activities of sucrose degrading enzymes

Since respiration in sugarbeet is fueled principally by the oxidative degradation of sucrose (Barbour and Wang, 1961) and begins with the enzymatic degradation of sucrose into its constituent monosaccharides, the activities of the three enzymes responsible for sucrose degradation – sucrose synthase, acid invertase, and alkaline invertase – were determined. Sucrolytic activities were unaffected by relative humidity during 28 d in storage (Fig. 7). No significant differences in sucrose synthase, alkaline invertase and acid invertase activities were observed between roots stored for 2 or 4 weeks at 40 and 85% relative humidity for either sugarbeet variety. Previously, Sakalo and Tyltu (1997) reported an increase in sucrose synthase activity and a transient increase in alkaline invertase activity in response to weight loss in sugarbeet roots stored at 20–23 °C and 75–85% relative humidity. The cause for the discrepancy in results between this and the earlier study are unknown, although storage temperatures differed in the two studies.

That relative humidity during storage had no effect on any sucrolytic activity suggests that dehydration or the membrane damage caused by dehydration does not induce or repress any sucrolytic activity in stored sugarbeet roots. This contrasts with reports in other plant species and organs of dehydration-associated increases in sucrose synthase expression (Kleines et al., 1999; Baud et al., 2004; Hazen et al., 2005) or decreases in soluble acid invertase expression (Andersen et al., 2002; Nayyar et al., 2006). However, induction of sucrose synthase expression and repression of acid invertase expression in response to dehydration are not universally observed in plants, since no change in expression or opposing changes in expression have been reported in many plant species or organs (Gordon et al., 1997; Wardlaw and Willenbrink, 2000; Hockema and Etxeberria, 2001). Similar to the results of the present study, sugarbeet sucrose synthase activity was previously found to be unresponsive to other postharvest stresses including cold temperatures, anoxic conditions or injury (Klotz and Haagenson, 2008).

Since sucrolytic activities were unchanged in sugarbeet roots subjected to dehydrating storage conditions, sucrolytic activities were apparently present in the root at time of harvest in quantities

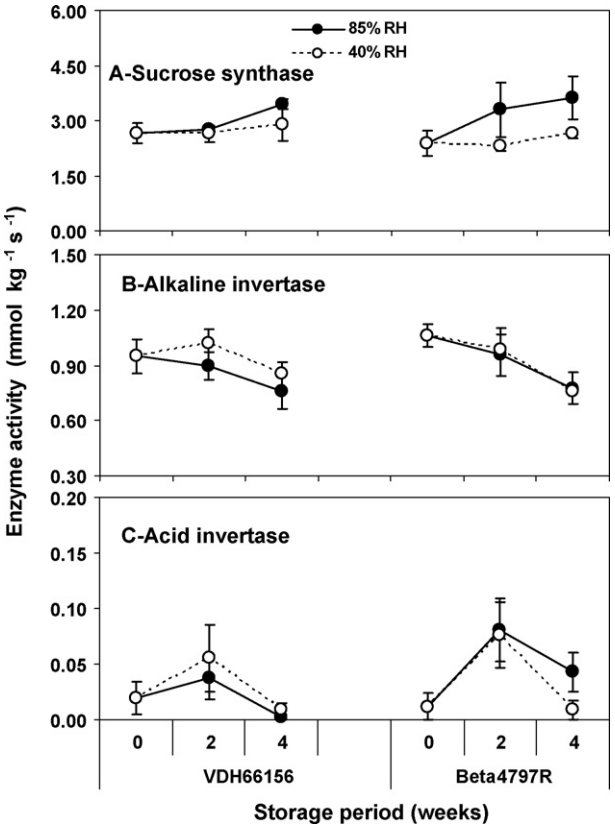

Fig. 7. Activities of the sucrolytic enzymes, sucrose synthase (A), alkaline invertase (B), and soluble acid invertase (C), in roots of two sugarbeet varieties, VDH 66156 and Beta 4797R, during storage at 85 and 40% relative humidity and 10 °C for 4 weeks. Activity is expressed as the rate of molecules of sucrose cleaved per mass of protein, $mmol\,kg^{-1}\,s^{-1}$. Data are the mean ± SE of the mean ($n = 4$). $LSD_{.05}$ for VDH 66156 and Beta 4797R, in panel A: 0.81, 1.31; panel B: 0.21, 0.25; panel C: 0.051, 0.059.

that were sufficient to meet the increased demand for respiratory substrates caused by dehydration. An additional demand for glycolytic intermediates was also likely to have been created by the membrane damage caused by dehydration and the repair mechanisms it invokes, although glycolytic intermediates were apparently provided without an increase in sucrose-degrading activity. These results are consistent with those of an earlier study that found that sugarbeet root sucrolytic activities at time of harvest were capable of providing the substrates needed for wound-healing processes and respiratory increases caused by severe root injury (Klotz et al., 2006).

4. Conclusions

Dehydration is common in postharvest sugarbeet roots and is known to increase sucrose loss during storage. Here, we demonstrate that dehydration is associated with an increase in root respiration. The increase in respiration observed in this study accounts for at least some of the sucrose loss that has been reported in dehydrated roots during storage. Unknown, however, is the proportion of dehydration-associated sucrose loss that is attributable to elevations in respiration rate, since sucrose is lost not only to respiration, but also to conversion to other carbohydrates, and to storage rots and diseases. Although genotypic differences in the magnitude of dehydration-associated increases in respiration rate were observed, respiration rate generally increased in association with increases in root weight loss and electrolyte leakage, an indicator of membrane integrity. Respiration rate, however, was most closely associated with electrolyte leakage, suggesting that

elevations in respiration rate were not due to dehydration, but to the membrane damage that occurred in response to dehydration. Since activities of sucrose-degrading enzymes were unaltered by dehydration, dehydration-associated elevations in respiration rate did not require additional sucrolytic activity to provide for the increased demand for respiratory substrates.

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